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Social Insects: Are Ants Just Wingless Bees?

New phylogenomic analyses suggest that ants and Apoidea (hunting wasps and bees) are more closely related than we had previously believed.

Bryan N. Danforth

Wasps, bees, and ants — the stinging Hymenoptera — are an extraordinarily important group for understanding the evolutionary history of eusociality, its origins and its loss.
Eusociality — typically defined by the combination of overlapping generations, cooperative brood care, and reproductive division of labor — is a remarkable evolutionary innovation. Some individuals, the workers, forego their own direct reproduction to serve as nurses, guards, foragers and caretakers for the offspring of a single reproductive individual, the queen. Eusociality in Hymenoptera is restricted to stinging wasps, ants and bees, the groups referred to as 'Aculeata'. Eusocial taxa in Aculeata include the ants (Formicidae [1]), vespid wasps (Stenogastrinae, Vespinae and Polistinae [2]), certain bee groups (Allodapini, Halictinae, and corbiculate Apidae [3]), and *Microstigmus* wasps (Crabronidae: Pemphredoninae [4]). A significant amount of work has focused on understanding phylogenetic relationships *within* these diverse eusocial lineages [3,5–9] because phylogenies provide an essential framework for inferring the evolutionary history of eusociality. A recent study in *Current Biology* by Johnson *et al.* [10], based on a massive data set of transcriptomes and whole genomes, provides some remarkable new insights into the relationships among the major branches of the aculeate tree of life, and thus sheds light on the evolutionary history of eusociality in the group as a whole.

Before molecular data were used to derive phylogenetic tress for wasps, bees and ants — i.e. before the early 1990s — the predominant view was that eusociality in Hymenoptera had arisen frequently (i.e., tens to hundreds of times) across Aculeata. However, subsequent molecular phylogenetic studies have suggested a contrary view: eusociality has arisen rarely in bees and wasps, but reversals from eusociality back to solitary nesting are common — rather than frequent origins explaining the diversity of social behavior, frequent losses of eusociality (or reversals to solitary nesting) provide much of the variation in sociality among closely related taxa. Eusociality has been repeatedly lost in clades of ancestrally eusocial halictine bees [9], and reversals appear to be associated with species and populations at high elevations or latitudes [7]. Recent studies of tribal relationships in the largely social Xylocopinae (carpenter and allodapine bees) [11] have also supported the hypothesis of a reversal to solitary nesting in one of the four xylocopine tribes: Manueliini. And recent molecular studies of corbiculate bees (honey bees and their relatives) have indicated that the weakly social orchid bees are likely derived from a primitively eusocial ancestor [12]. While phylogenetic studies have primarily been carried out on eusocial groups, such as Vespidae, Xylocopinae, Halictinae, and corbiculate Apidae, few studies have tackled the higher-level relationships among the major clades of Aculeata, and these studies have been based on a relatively small number of 'standard' phylogenetic markers [13,14]. No previous studies have attempted to analyze aculeate relationships based on much larger transcriptomic or genomic level data sets.

Phylogenomics — the application of large-scale (transcriptomic or genomic) data sets to phylogeny reconstruction — has the potential to revolutionize the way we do phylogenetic studies. Rather than analyze a small set of previously defined genes, high-throughput sequencing methods allow for more expansive coverage of mitochondrial genomes, expressed genes, conserved regions of whole genomes, and whole genomes [15–19]. Phylogenomic studies can be based on hundreds to thousands of genes. While these methods have enormous potential for phylogenetic analysis, they also pose some serious challenges. Assembly and annotation of non-model genomes can be difficult. Determining which genes are true orthologues when conducting multiple alignments in non-model organisms can also introduce problems in downstream analysis. Finally, such methods tend to put substantial limits on taxon sampling, which we know is key to accurate phylogenetic resolution.

Johnson and co-authors [10] apply combined genomic and transcriptomic data to the higher-level phylogeny of Aculeata. Their data set is derived from previously published genomes of three bee and three ant species, plus *de novo* transcriptome data for ten additional taxa spanning nine aculeate wasp families. The published genome of the parasitic wasp *Nasonia vitripennis* was used as an outgroup. Based on bioinformatic analysis of the transcriptome and genome data, they obtained multiple partitioned amino acid matrices ranging from 300 genes

(over 175,000 amino acid sites) to over 5000 genes (over 3 million amino acid sites). Based on partitioned maximum likelihood and Bayesian analyses of their data sets, they obtained a strongly supported tree (all nodes are supported by 100% likelihood bootstrap values and a posterior probability of 1.0). All analyses supported a novel result: ants and Apoidea — the clade that includes four solitary hunting wasp families plus the bees — are sister groups. Previous studies, based on both morphology [20] and molecular data [13,14] had suggested that ants were more closely related to ectoparasitic wasps (such as Scoliidae, Tiphiidae, and Bradynobaenidae) than to the clade that includes hunting wasps and bees (Apoidea). Johnson and co-authors' analysis [10] suggests otherwise. Apoidea (including hunting wasps in the families Heterogynaeidae, Ampulicidae, Sphecidae, and Crabronidae, plus bees) and Formicidae appear to be sister groups. Likelihood-based methods for evaluating alternative hypotheses indicate that their data set can significantly reject alternative topologies, further supporting the view that their results are robust to changes in tree topology. Vespidae, the other major clade of eusocial aculeates, arises as sister to all Aculeata excluding Chrysidoidea, indicating that vespid wasps are distantly related to ants and Apoidea. While nodal support in their tree is high based on bootstrap proportions and posterior probabilities, sparse taxon sampling and a distantly related outgroup might just be leading to incorrect, but strongly supported, phylogenetic conclusions. Future studies with broader taxonomic coverage will provide additional tests of this hypothesis.

If true, the close phylogenetic affinities of ants and Apoidea would have significant implications for understanding the evolutionary origins and prerequisites for eusociality. Ants, Apoidea, and Vespidae are all groups in which females construct a nest to which prey (or pollen) is transported. Hunting wasps (and bees) are behaviorally sophisticated central-place foragers that must fabricate a nest from soil or other materials, learn landmarks associated with the location and chemical cues associated with the identity of their nest, transport prey (or pollen) over long distances, and defend the nest against predators and parasites. Nest construction, provisioning, and central-place foraging have been identified as potential prerequisites for the evolutionary origins of eusociality — a view supported by Johnson *et al.*'s [10] analysis. While the new phylgenomic results contradict previous molecular and morphological studies in terms of the affinities of ants and Apoidea, a recently described fossil [10] that has been alternatively placed in the ants and the basal Apoidea (Ampulicidae) might suggest that ants and Apoidea are more closely related than we had previously believed. This might just be a case where fossils and genomes converge on the same radical, anti-establishment view of aculeate phylogeny.

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Stress Response: Anything that Doesn't Kill You Makes You Stronger

A new study shows that DNA damage not only elicits response pathways directly related to DNA repair but also induces a response that extensively overlaps with the pathogen infection pathway and confers resistance to both oxidative stress and heat shock.

Anton Gartner[1,*] and Alper Akay[2]

Hormesis occurs when a low-level stress elicits responses that protect against subsequent exposure to severe stress. Such protection often affects a variety of stress conditions. For instance, oxidative and thermal stress